moving animals makes for an exciting time in systems neuroscience. While many challenges undoubtedly lie ahead, especially as we confront the dizzying complexity of spatial codes and grapple with turning neural correlates into mechanistic hypotheses, so do many opportunities for new insight.

DECLARATION OF INTERESTS

The author declares no competing interests.

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Biogeography: The origin and spread of bee lineages

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Where and when bees originated and how they dispersed and diversified across ancient continents has remained ambiguous. A new study that combines phylogenetics with fossil data reconstructs the origin and diversification of bees across geological time and space.

With more than 20,000 species worldwide, bees are the most prominent and specialized insect pollinators on Earth. The intricate association between bees and flowering plants, which began sometime during the mid-Cretaceous, has produced magnificent adaptations on both sides of this ancient liaison. Bees exhibit astonishingly diverse behaviors, including solitary nesting, brood parasitism, social parasitism and eusociality. Moreover, bees have evolved numerous adaptations for foraging, navigation, cognition, communication, brood provisioning and host-plant specialization. However, despite the importance of bees in the evolution and maintenance of modern plant biodiversity, their origin and early evolution have remained obscure due to their sparse fossil record. A new study by Almeida, Bossert *et al.*[1] in this issue of *Current Biology* presents a comprehensive phylogenomic reconstruction coupled with a biogeographic analysis of all major bee groups. Their detailed analysis reconstructs when and where bees originated and how different lineages dispersed and diversified across ancient continents in geological time.

Bees belong to one of the largest groups of insects — the order Hymenoptera — along with ants, hunting wasps, parasitic wasps and sawflies[2,3]. Although bees depend entirely on pollen and nectar gathered from flowers to feed their larvae, the closest relatives of bees consist of a small group of hunting wasps that specializes in catching insect prey[4]. Bees, therefore, originated when an ancestral carnivorous wasp lineage transitioned into a vegan lifestyle.

But when and where did this evolutionary transition take place? What ecological conditions and habitats

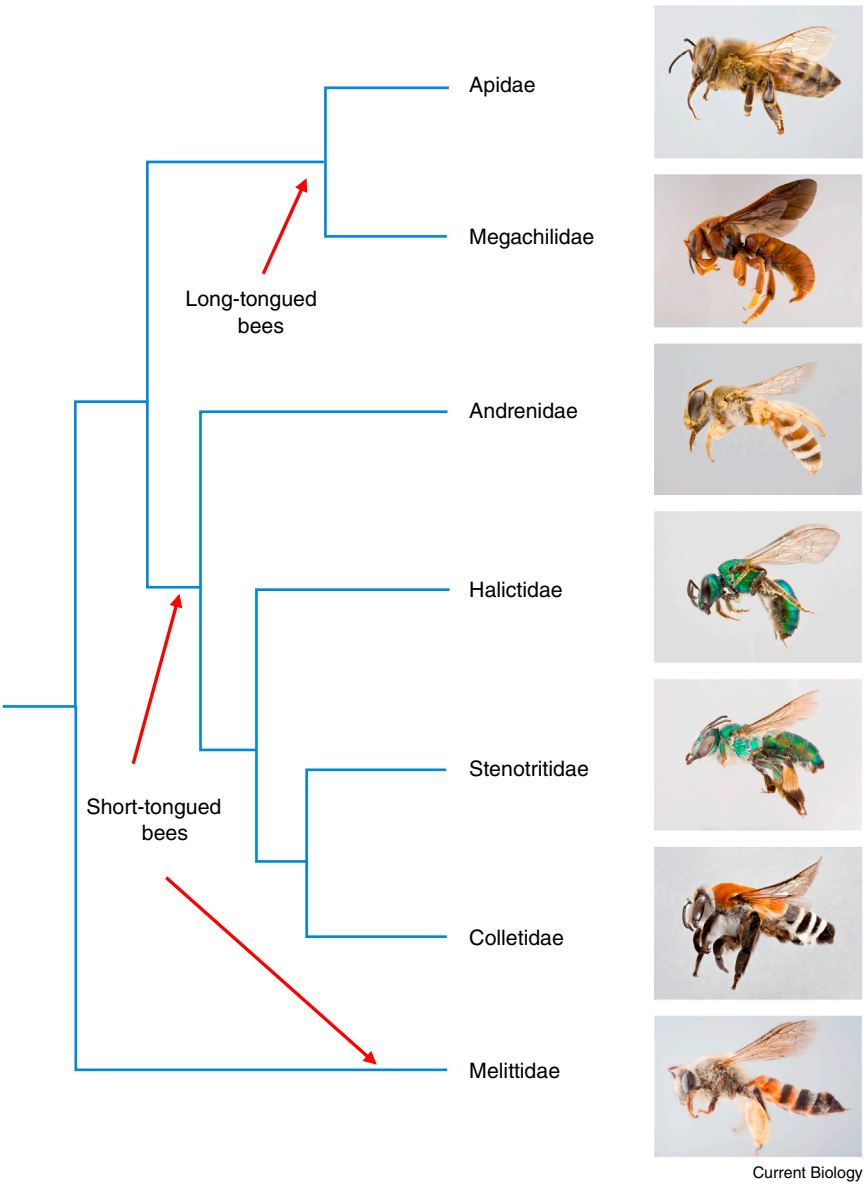

Figure 1. A family-level phylogenetic tree of bees.
Bees include the most important and specialized insect pollinators on Earth. With more than 20,000 species worldwide, the evolutionary relationships of major bee lineages has remained ambiguous. Recent phylogenetic studies have resolved the evolutionary relationships among major bee groups, including the seven bee families depicted here. Having a clear picture of the phylogenetic relationships of major bee groups, and a reliable estimate for when ancestral bee lineages existed, allowed Almeida, Bossert *et al.*[1] to infer the place of origin of modern bees and reconstruct when and how different bee lineages colonized ancient landmasses in geological time. Images obtained from Laurence Packer's website (https://www.yorku.ca/bugsrus/resources/resources) with assistance from Cecily and Robert Bradshaw.

favored the origin and diversification of bees? How and when did different bee lineages colonize Earth's ancient continents and regions? When and where did the different types of social behavior evolve? How did the intimate association between bees and insect-pollinated angiosperms unfold to produce the remarkable diversity we observe today?

Answering these questions requires resolving the phylogenetic relationships of major bee groups and having reliable estimates for when ancestral bee lineages existed.

To find out when and where the common ancestor of modern bees lived, and how they subsequently dispersed across landmasses, Almeida, Bossert and colleagues conducted a series of analyses, each building upon the previous one. First, they built the most comprehensive phylogenetic tree of extant bees to date by assembling ~800 genomic regions known as ultra-conserved elements (UCEs) across 216 species strategically scattered across the bee phylogeny. The resulting phylogeny is largely congruent with recent phylogenetic studies[5–9]. Although our understanding of bee evolutionary relationships has changed dramatically in the past 20 years since genomic tools became readily available[10], it appears that the bee phylogeny presented by Almeida, Bossert *et al.* finally represents a stable hypothesis (Figure 1), at least at the family and tribe levels.

In the next step, Almeida, Bossert *et al.* curated all known bee fossils and selected a subset of 185 records that can be assigned with confidence to modern bee groups. These fossils, and their geological ages, were used to calibrate a molecular clock using a 'fossilized birth–death' model, a Bayesian framework that combines fossils and extant DNA sequences to model a unified diversification process[11]. This analysis produced a time-calibrated tree that suggests the common ancestor of modern bees lived ~124 million years ago, with a confidence interval of 106–139 million years. Their molecular clock analysis also revealed that all modern bee families — except for the rare bee family Strenotritidae that only lives in Australia — originated prior to the Cretaceous–Paleogene (K–Pg) boundary, the time when dinosaurs went extinct 65.6 million years ago. Similar to the phylogenetic analysis, these age estimates are congruent with other recent molecular clock studies[5,10].

With a time-calibrated tree on hand, the authors proceeded to investigate the ancient biogeography of bees. The lofty goal of this analysis is to infer the place of origin of modern bees and reconstruct when and how bee lineages colonized ancient landmasses, for which the authors used a dispersal-extinction-cladogenesis (DEC) model. This method incorporates geological information, like plate tectonics or the configuration of ancient continents, to define dispersal probabilities between ancient landmasses across geological time. This

requires encoding a dispersal probability matrix by examining geological records and identifying the time windows when continents were connected by land bridges or separated by oceans. The authors encoded dispersal probabilities for six world regions, including Afrotropical, Australian, Nearctic, Neotropical, Oriental and Palearctic, across six geological time slices. But defining these dispersal probabilities for long extinct lineages across ancient continents is challenging. The authors then encoded different versions of these probability matrices, ranging from more restrictive to less restrictive dispersal probabilities.

The results of this type of biogeographic analysis can reveal whether a particular ancestral branch along the bee phylogeny — for example, an ancestral representative of the family Megachilidae — was present in a particular landmass during a specific geological period. Moreover, these results can reveal when and how different bee lineages dispersed across ancient continents. Their analysis pinpointed Western Gondwana as the most likely region where bees originated during the mid-Cretaceous. Remarkably, Charles Michener, a prolific bee biologist and taxonomist[12], reached a similar conclusion in 1979[13], even though at the time he had the wrong phylogenetic tree and did not have access to a time-calibrated phylogeny, and modern biogeographic tools were unavailable. Michener's insightful analysis relied on the biogeographic distribution of what he considered the earliest branching bee group, the cellophane bees in the family Colletidae, and the intriguing disjunct geographical distribution of these bees in southern continents that previously formed Gondwana. The convergence on a mid-Cretaceous Western Gondwana as the time and place of origin for bees poses a compelling scenario, though it should be taken with caution. No bee fossils have been recovered from geological deposits in this region from this geological period, and the earliest putative bee fossil, a ~100 million year old Burmese amber inclusion, cannot be assigned to any modern bee group[14].

The Gondwana supercontinent included landmasses that today correspond to South America, Africa, Antarctica, Australia and India. Western Gondwana has been inferred as having a dry and arid climate[15,16]. Interestingly, the modern bee diversity hotspots are located in places with dry climatic conditions around the world[17]. If correct, the conclusion reached by Almeida, Bossert *et al.* begs the question of why arid habitats favored the origin of bees in the past, and today similar habitats harbor the highest bee diversity. This observation may represent an exceptional case of long-term niche conservatism, but alternative explanations need to be evaluated.

The biogeographic analysis presented by Almeida, Bossert *et al.* also reveals that when South America and Africa began drifting apart, 80–100 million years ago, ancient representatives of the long-tongued bee families Apidae and Megachilidae were likely present on both continents. In turn, they infer that this continental split left other bee families, like the sweat bees (Halictidae), the cellophane bees (Colletidae) and the mining bees (Andrenidae), restricted to South America only. The earliest-branching bee family Melittidae remained in Africa, where the group is most diverse today. At this time, no bee lineages had reached Australia, and India remained 'bee free' until it collided with Asia. This is consistent with the observation that no ancient endemic bee lineages inhabit India today.

Towards the Late Cretaceous, ~80 million years ago, all modern bee families (except Stenotritidae) had originated and started to disperse across the Southern continents of Gondwanaland, including South America, Africa and Australia. The cellophane bees, a diverse group of strictly solitary bees, likely originated in South America and later colonized Australia, where they diversified extensively. In fact, half of the Australian bee fauna today belongs to this bee family. Other bee families likely arrived much later to Australia, but other bee groups, like bumble bees of the family Apidae with a global distribution, never reached Australia.

Finally, it wasn't until more recent times, 40–60 million years ago, that bees started to colonize the northern hemisphere. The authors report that this northward expansion was revealed by the combination of the DEC model-based reconstruction and the geographic distribution of bee fossils. During this period the Earth experienced a warmer climate that permitted the expansion of tropical bee lineages, like stingless bees, into northern latitudes. In fact, stingless bees, which are otherwise exclusively tropical at present, are found in fossil deposits from both North America and Europe, where they are now extinct.

Because bees depend exclusively on flowering plants for food, and many flowering plant lineages have evolved specialized floral traits for bee pollination, the evolutionary history of these two groups is undoubtedly highly intertwined. However, the lack of equivalent biogeographic inferences for plants in the mid-Cretaceous prevents making a side-by-side comparison of biogeography of both bees and flowering plants. As the authors write, the work should invite close examination for how bees and flowers coevolved in both space and time.

Bee pollinators have profoundly influenced the evolution of plant diversity since the mid-Cretaceous. Today, bees and other insect pollinators play a critical ecological role, including the maintenance of plant populations in natural habitats and ensuring food security in agricultural ecosystems. The work by Almeida, Bossert *et al.* will facilitate future studies on the ecology, evolution and conservation of bees and pollination biology. Several studies have shown that bee populations around the world are experiencing declines at alarming rates due to various stressors, including pesticide use, lack of suitable habitat and pathogen spillover. However, these population declines are non-random with respect to phylogeny, biological traits and geography. For example, a recent study found that climate warming caused substantial body-size shrinking in a community of solitary bees from a preserved area in Spain over a 30-year period. In that study larger bees and cavity-nesting bees experienced more pronounced body-size declines than smaller bees and ground nesting bees, respectively[18]. In contrast, a census of orchid bee communities from preserved areas in tropical lowland rainforests of central Panama found neither population declines nor body mass changes over a 40-year period[19]. Global phylogenetic trees, like the one presented by Almeida, Bossert *et al.*, will improve our predictive power of the

factors, traits, geographic distributions and phylogenetic relationships that make certain species or lineages more susceptible to different types of stressors.

DECLARATION OF INTERESTS

The author declares no competing interests.

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Climate change: Shifts in time between flowering and leaf-out are complex and consequential

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A new study investigated how time intervals between flowering and leaf-out in woody plants are impacted by climate change. Climate change has shifted the timing of both stages, but its impact on the interval between them is complex and variable.

In basic models of plant development, vegetative growth precedes reproduction. However, long-lived perennial trees and shrubs can deviate from this typical developmental schedule by drawing on stored energy from previous seasons, and the woody plant species that comprise temperate forests around the globe display tremendous variation in the sequence in which their flowers and leaves emerge each spring[1] (Figure 1A,B). While we have long known that phenology — the timing of seasonal life-cycle events like flowering and leaf-out — is critical to both the fitness of individuals and functioning of ecological communities, more recent evidence suggests that it is not only the absolute timing of these individual stages, but their order and relative timing, that is under selection to maximize plant fitness[2]. This